NICHE RELATIONSHIPS OF *THAMNOPHIS RADIX HAYDENI* AND *THAMNOPHIS SIRTALIS PARIETALIS* IN THE INTERLAKE DISTRICT OF MANITOBA

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ABSTRACT

The niches occupied by the western plains garter snake (*Thamnophis radix haydeni*) and the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake district of Manitoba were compared with respect to feeding habits and six environmental factors. The species were studied both in allopatry and in sympatry.

Thamnophis sirtalis occurring in sympatry with *T. radix* altered its feeding habits, but not in such a way as to produce niche displacement. Its feeding habits did not differ significantly from those of *T. radix* either in allopatry or in sympatry. Changes in its feeding habits are attributed to changed in the relative availability of food items.

Of the environmental factors examined, habitat, air temperature and substrate temperature contributed most strongly to niche discrimination in allopatry. *Thamnophis radix* occurred near meadow ponds at high air but low substrate temperatures and *T. sirtalis* occurred near fen-like marshes of the aspen forest at lower air but higher substrate temperatures. In sympatry the contributions of habitat and air temperature to niche discrimination were reduced, whereas those of light intensity and substrate temperature were increased, *T. radix* selecting a higher value of both than *T. sirtalis*. This shift in the importance of environmental factors to niche discrimination need not be attributed to species interaction but may be explained in terms of behavioral compensation for concurrent changes in the available niche. The shift was partially produced by changes in the daily activity pattern, towards midday for *T. radix* and towards morning and evening for *T. sirtalis*.

INTRODUCTION

The summer niche requirements of garter snakes are poorly known and the degree of competitive interaction between species is not known at all. Food and habitat utilization (Carpenter, 1952; Fleharty, 1967) and food utilization (Fouquette, 1954) have been compared for sympatric populations of garter snakes species in three widely separated localities. None of these authors, however, obtained detailed comparative data for allopatric populations of the same species. Niche displacement among sympatric garter snakes, while suggested by these authors as a possible explanation for resource partitioning, has seldom been properly examined. A notable exception is the work of White and Kolb (1974) on sympatric populations of two garter snake species in California, one of which is represented by a nearby allopatric population.

In the Interlake district of Manitoba two garter snake species occur: the western plains garter snake (*Thamnophis radix haydeni* Kennicott) and the red-sided garter snake (*Thamnophis sirtalis parietalis* Say). While the range of overlap between these species is limited, both occur in sufficiently large numbers to allow the collection of adequate samples from within this range. The present study compares the niches occupied by these two species, both within the range of overlap and beyond it, to determine whether any changes in the relative niche positions were occurring that could be attributed to the presence or absence of a congeneric species rather than to changes in the available niche.

MATERIALS AND METHODS

Field Study. – The study area is located approximately between 50° N and 51° N latitude and between 97° W and 98° W longitude. It is bounded on the east by Lake Winnipeg and on the west by Lake Manitoba as outlined in Figure 1. Snakes were captured within this area from May through August of 1973 and from June through August of 1974. The sampling effort in 1974 was concentrated within a region defined on the basis of the first summer's sampling and included all quarter-townships (23.4 km²) in which both *T. radix* and *T. sirtalis* had been captured. This region of sympatry is shown in Figure 1. Severe flooding in May of 1974 prevented sampling before June.

Snakes were found by searching on foot in the vicinity of water and were captured by hand. Preliminary sampling had shown that garter snakes in the Interlake district were seldom found far from a water body of some sort. Snakes seen crossing roads were not captured since the road habitat is not a natural one and cannot be avoided by snakes in their movements. The sampling effort was spread over the daylight hours from sunrise to sunset since preliminary attempts to find snakes at night had proven unproductive. No systematic sampling plan was followed due to the difficulty of collecting large samples without being somewhat opportunistic in allocation of the sampling effort. Any developing bias in collection with respect to time of day, geography or weather condi-
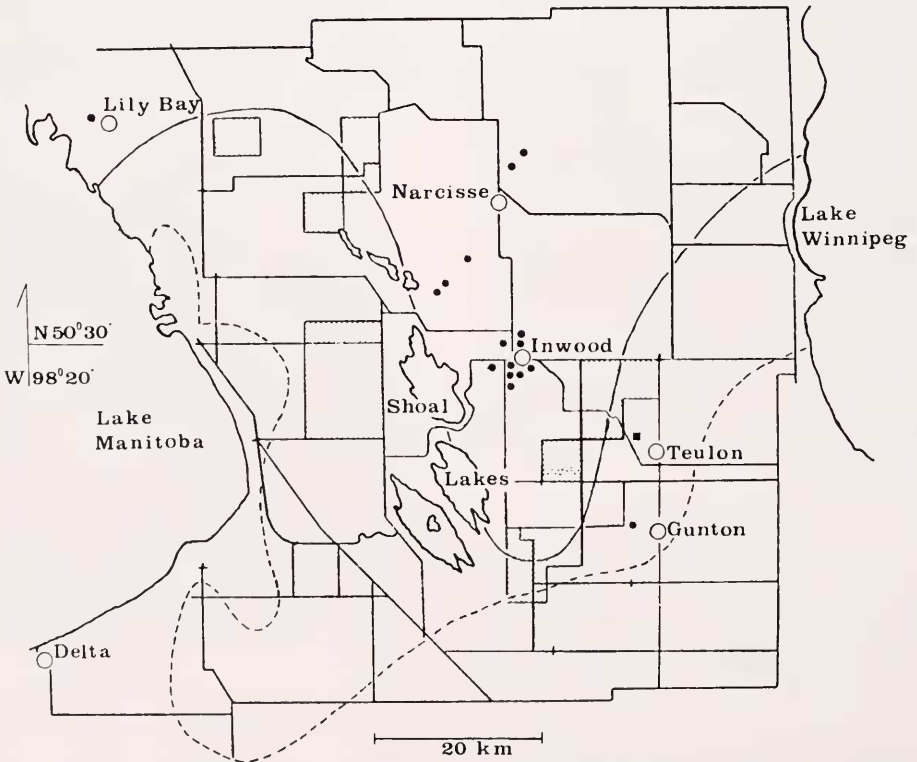

Fig. 1. Map of the study area showing major roads, towns (open circles) and approximate lines of continuous (solid) and discontinuous (dashed) aspen forest. Areas included in the sympatric region are stippled. All other areas are included in the allopatric region. The known communal den of *T. radix* (solid square) and known communal dens of *T. sirtalis* (solid circles) are located.

tions was soon detected from field records and appropriate corrections were made.

The feeding habits of *T. radix* and *T. sirtalis* were examined by palpating the stomachs of all snakes captured to force regurgitation of recently eaten food. Due to the difficulty of determining the number of prey represented in partially digested remains, only the presence, and not the number, of food items of each type found in a snake was recorded.

Six environmental factors were recorded at all capture sites to determine the relative importance of each of these factors as niche dimensions. A niche dimension is defined here as any factor serving to separate species ecologically (Levins, 1968) and the importance of an environmental factor refers here to its value in separating *T. radix* and *T. sirtalis* ecologically. Since biotic, physical and temporal environmental factors were considered, the term "environmental factors" is used in its broadest sense. However, the environmental factors considered were all judged capable, a priori, of eliciting direct response from a snake.

Habitat was classified as an environmental factor according to the type of water body nearest the capture site of a snake. Water was usually available within several hundred meters of a capture site. Three habitat classes that reflected the proportion of water surface area covered by a sedge mat were recognized. A sedge mat was composed of moss and old sedge decaying just beneath the surface of the water and was overlain by the previous year's growth of sedge, which was folded to form a compact horizontal network at or above the surface of the water. Habitat classes included ponds (no sedge mat; sharp interface between land and water), open marshes (sedge mat at the edges only; open water or sparse emergent vegetation dominant) and closed marshes (dominated by sedge mat; little or no open water). The terminology of aquatic communities in the aspen forest and parkland has not been standardized. Ponds in the study area conformed to the definition of

Radforth (1964). Cover was readily available only in the form of shrubbery or small mammal burrows. Large rocks and logs were rare and did not seem to be used for cover. Heinselman (1963) included the marsh types referred to here as open and closed in his definition of marsh. Closed marshes in the study area resembled fens but were neither sufficiently peaty nor sufficiently patterned to conform well to Heinselman's definition of that term. Cover was readily available in the form of sedge mat and encroaching aspen forest. Habitat classes were coded in the above order from 1 through 3. They were judged to be sufficiently discrete in nature to warrant the use of a discrete variable as a numerical code. A transition from the first habitat class to the last was apparent on a south-west to north-east cline through the study area and corresponded to a transition from parkland to aspen forest.

Substrate moisture was classified as an environmental factor on the basis of a simple test performed at the capture site of a snake. If water could not be forced through the fingers by pressing the back of the hand against the substrate with as much force as possible, the substrate was termed dry. If water could just be forced through the fingers by similar action, the substrate was termed damp. If the cup of the hand could be filled with water by similar action, the substrate was termed waterlogged. Two additional moisture classes included standing water (with emergent vegetation) and open water (with no emergent vegetation). Moisture classes were coded in the above order from 1 through 5. This crude method of quantifying substrate moisture seemed to correlate well with the amount of water at the surface although it was certainly not a perfect linear measure. It was considered preferable to measurements of water content from soil samples since the latter reflected moisture beneath the surface, which often differed markedly from that found at the surface.

Light intensity incident upon the snake at the precise point where it was originally

seen was measured as an environmental factor with a Vivitar photographic light meter (Model 43). The meter was sensitive only to visible light. Intensity was recorded in units of exposure value (EV) at an ASA setting of 100 with the light meter pointed directly at the sun.

Air temperature at substrate level was recorded at all capture sites with Yellow Springs Incorporated (YSI) thermistors (Models 43TD and 42SC) and YSI probes (Model 402). The probe was held in the body shadow of the investigator as close to the substrate surface as possible without contact.

Substrate temperature was recorded at all capture sites with the same thermistors. Since substrate temperature near the surface was extremely sensitive to the depth and exact location of the thermistor probe, temperatures were taken at a depth of 5 cm below the surface. Although this procedure minimized measurement error due to minor variations in probe position it must be noted that temperatures at this depth often differ from those experienced by a snake at the contact surface. When snakes were found upon a vegetation mat the surface was defined at the level of the highest part of the snake's body that was in contact with the vegetation.

Time of capture of each snake was recorded as an environmental factor on the daylight-saving time scale. It was coded as an absolute deviation (in hours) from 1400 hours (2 P.M. and the approximate midpoint of the day) so as to reflect the degree of mid-day activity of the snakes. No distinction was made with this time scale between morning and evening, so that the scale would correlate roughly with diel variations in environmental temperature and light intensity. Such a scale was desirable in order that the degree of correlation of time of capture with temperature or light intensity at capture sites would serve as an indicator of the extent to which snakes were making use of diel variations in selecting environmental temperatures or light intensities.

The six environmental factors described above were felt to be of potential importance in characterizing and distinguishing between the niches of *T. radix* and *T. sirtalis*. For an environmental factor to be important in this sense it is necessary, though not sufficient, that the snakes be sensitive to it. One way in which all of the environmental factors measured seemed potentially capable of affecting a snake was by means of influencing its body temperature. To detect such influences both oral and cloacal body temperatures of the snakes were taken along with measurements of the six environmental factors at each capture site. The same thermistors used to record air and substrate temperatures were used for this purpose. Body temperatures were always taken immediately upon capture and with minimal handling of the animals. The two body temperatures were taken consecutively and in no particular order.

Data of the type described above were taken from snakes captured in allopatric and sympatric regions in the summer of 1973. An additional sample of snakes was collected from within the sympatric region in the summer of 1974. Data from this sample were pooled with those taken from the same region the year before.

Analytical Methods. —Feeding habits of *T. radix* and *T. sirtalis* were compared, both in allopatric and in sympatric regions, using a 2xC contingency chi-square test for association between species and food type utilized. Feeding habits in allopatric and sympatric regions were also compared, both for *T. radix* and *T. sirtalis*, using a 2xC contingency chi-square test for association between region and food type utilized. Columns were pooled in all contingency tables to produce expected values greater than 1.

Sampling effort in the field was estimated for each species in hours spent searching for snakes within its range. Daily profiles of catch per unit effort, calculated for hourly intervals throughout the course of the day, were compared between *T. radix* and *T. sirtalis* both in allopatric and in

sympatric regions. For intervals in which less than three search hours had been spent catch per unit effort was not calculated.

Slight biases often developed in the sampling effort before they were noticed and corrected. The effort spent searching for *T. radix* and *T. sirtalis* varied slightly throughout the summer in favor of either one species or the other. Since the range of environmental factors available to the snakes also varied throughout the course of the summer, such disparate seasonal allocation of the sampling effort was likely to produce spurious differences between species in the range of environmental factors measured at capture sites. Therefore, seasonal trends in environmental factors were quantified so that environmental data from capture sites could be adjusted for these trends by covariance, using powers of the date (day of the year and day^2) as covariates. This method of compensating for seasonal effects in long term data was used by Green (1974) in a similar type of study. It allowed description of seasonal trends in the environmental factors as parabolic curves. On the basis of visual inspection of the scatter of points about these curves, this description was considered to be adequate.

The frequency distributions of environmental factors were often non-normal. Medians often differed significantly from the means indicating skewness, and 95% confidence intervals on individual observations often exceeded or fell short of the measured range indicating kurtosis. With large samples non-normality has little effect upon comparisons of the means either by univariate (Scheffe, 1959) or by multivariate (Ito *in* Krishnaiah, 1969) methods, although it may influence comparisons of variance and covariance more strongly. Heterogeneity of variance, which often accompanies non-normality, was considered more of a problem. Press (1972) cautions that although univariate comparisons of means are little affected by heterogeneity of variance when sample sizes are large, most assertions about robustness

with respect to the assumption of homogeneity of variance in the multivariate case are speculative. The reliability of multivariate methods must therefore be considered uncertain to the extent that this assumption is violated. Adjustment of environmental data for seasonal trends, as described above, improved multivariate homogeneity of variance and covariance in the present study.

The means of environmental factors for *T. radix* and *T. sirtalis* were compared both by univariate and multivariate methods. Large sample normal deviate tests were used for univariate comparisons. These were applied to environmental data that had not been adjusted for seasonal trends since the seasonal trends shown by two of the environmental factors differed significantly between species. In these cases the description and use of common seasonal trends to adjust the environmental data for long term effects was not strictly justified. Discriminant function analysis (Cooley and Lohnes, 1971) was used for multivariate comparison of environmental factors between *T. radix* and *T. sirtalis*. Environmental data for use in discriminant function analysis were adjusted for seasonal trends since this procedure improved multivariate homogeneity of variance and covariance. The use of seasonally adjusted data may have been somewhat artificial since not all environmental factors showed seasonal trends that were common to both species. However, uncertainty about the robustness of multivariate methods to violations of the homogeneity of variance assumption made the use of seasonally adjusted environmental data preferable for multivariate comparison. Multivariate comparison was considered more informative than univariate comparison because it takes correlations between the environmental factors into consideration.

The method of discriminant analysis as used here is analogous to a multiple regression of a dependent variable reflecting species membership upon a set of environmental factors. Environmental factors

which contribute strongly to discrimination between the niches of *T. radix* and *T. sirtalis* are weighted heavily in the multiple regression equation, or discriminant function, so as to maximize the ratio of between species to within species variability in the predicted values of the dependent species variable. These predicted values are called discriminant scores. Each snake was therefore assigned a discriminant score which was a linear function of the environmental factors measured at its capture site. The difference between the mean discriminant score of *T. radix* and *T. sirtalis* is a measure of the overall ecological distance between their niches. An increase in this distance when snakes are collected from a region of sympatry can be taken as evidence of niche displacement.

The magnitude of the weight assigned to an environmental factor in the discriminant function depends not only upon the importance of that factor to species discrimination but also upon the magnitude of its measurement units. Standardization of all weights equalizes the scale of measurement so that the standardized weights represent the relative proportion of species discrimination contributed to the function by each environmental factor. Multiplication of these standardized weights by the discriminating power of the entire function gives an index of the ecological importance of each factor which can be compared between different discriminant functions. The measure of discriminating power used here was the squared canonical correlation coefficeint between the species variable and the environmental factors. This measure represents the fraction of variation in species membership explained by the discriminant function. The index so produced was used to compare the ecological importance of environmental factors between allopatric and sympatric regions. The sign of this index for any one factor indicated the relative position of *T. radix* and *T. sirtalis* on that environmental gradient. A negative sign indicated that *T. radix* was found at the lower end of that gradient and *T. sirtalis* at the upper end.

To determine the degree of dependence of body temperatures upon the environmental factors, multiple regressions of oral and cloacal temperatures on these factors were calculated separately for *T. radix* and *T. sirtalis*. Normal deviate tests were used to compare slopes and intercepts between species.

RESULTS

In the summer of 1973, 137 *T. radix* and 128 *T. sirtalis* were captured. Of these 32 *T. radix* and 36 *T. sirtalis* were found within the sympatric region. An additional sample of 73 *T. radix* and 32 *T. sirtalis* was collected from within the sympatric region in the summer of 1974.

Feeding Habits.—From Table 1 it was apparent that there were no differences in the feeding habits of *T. radix* and *T. sirtalis* either in the allopatric region ($X_7^2 = 9.66$; $P > .01$) or in the sympatric region ($X_6^2 = 10.47$; $P > .01$). The feeding habits of *T. radix* did not differ between allopatric and sympatric regions ($X_8^2 = 11.68$; $P > .01$). The feeding habits of *T. sirtalis* did differ between allopatric and sympatric regions ($X_4^2 = 13.42$; $P .01$). The change involved an increased utilization in the sympatric region of wood frogs (*Rana sylvatica*) and a decreased utilization of chorus frogs (*Pseudacris triseriata*).

Environmental Factors. — Seasonal trends in the environmental factors were adequately described as parabolic functions of the date. Habitat, as recorded at capture sites, was affected by seasonal movements of the snakes in the allopatric region. As *T. sirtalis* moved north in the fall towards its denning sites (Gregory and Stewart, 1975) it was found more frequently near the closed marshes of the aspen forest. A slight shift in *T. radix* towards the ponds of the open parkland to the south was not significant, but the trends for *T. radix* and *T. sirtalis* differed significantly from one another in the allo-

patric region. In the restricted sympatric region seasonal movements of the snakes had less effect on habitat classes and no significant seasonal trends were shown. Moisture, as recorded at capture sites, decreased throughout the summer in the allopatric region as water bodies dried up. In the sympatric region, flooding in the spring of 1974 increased July moisture levels at capture sites. This effect was not apparent until July because the flooding restricted snake collection in June. The effect was more pronounced for *T. radix* than *T. sirtalis* because the proportion of *T. sirtalis* taken in the sympatric region during the summer of 1974 was severely reduced due to drowning at dens in the spring. This produced significant differences between *T. radix* and *T. sirtalis* in the seasonal trends shown by moisture within the sympatric region, even though their individual trends were not significant. Light intensity decreased throughout the summer as the azimuth of the sun decreased. Air and substrate temperatures peaked in mid-summer. Time of capture of the snakes, expressed as a deviation from mid-day, showed no significant seasonal trends.

Univariate comparisons of environmental factor means between the niches of *T. radix* and *T. sirtalis*, applied to environmental data that had not been adjusted for seasonal trends, showed interspecific differences in habitat, moisture, air temperature and substrate temperature to be significant (P < .01) in the allopatric region (Fig. 2). Similar comparisons in the sympatric region showed significant (P. < .01) interspecific differences in habitat, light intensity and substrate temperature.

These differences remained apparent after adjustment of the environmental data for seasonal trends. Discriminant scores derived from seasonally adjusted environmental data gave better discrimination between the niches of *T. radix* and *T. sirtalis* than did any single environmental factor, both in allopatric and in sympatric regions, but did not give any evidence of niche displacement. On the contrary, discriminant scores became more similar in the sympatric region than in the allopatric region (Fig. 3). Multivariate results agreed well with those derived by univariate methods, although some differences were apparent (Table 2). The index of ecological importance, derived from the weights in the discriminant function, was large for habitat, both in allopatric and in sympatric regions, although it became smaller in the sympatric region, indicating reduced importance there. The negative sign of this index indicates that *T. radix* occupied the lower end of the habitat gradient (ponds) and *T. sirtalis* the upper end (closed marshes). Substrate moisture, in contrast to univariate results, was not ecologically important in either region. Light intensity was important only in the sympatric region with *T. radix* occupying the upper (sunny) end of the gradient whereas air temperature was important only in the allopatric region, with *T. radix* occupying the upper (warm) end of the gradient. Substrate temperature was important in both allopatric and sympatric regions, although it become more important in the latter region. Associated with the increased importance of this factor in the sympatric region, in contrast to univariate results, was a reversal in the relative species positions on the gradient, *T. radix* coming to occupy the upper (warm) rather than the lower (cool) end. Time of capture, expressed as a deviation from mid-day, was not an ecologically important factor in either the allopatric or the sympatric region. These results agree with those based on univariate comparisons, although in the sympatric region they give considerably less importance to the time factor.

Thermal Relations. — Oral and cloacal temperatures of *T. radix* were significantly higher (P < .01) than those of *T. sirtalis* in the allopatric region only. Body temperatures of *T. sirtalis* increased significantly (oral P < .05; cloacal P < .01) in the sympatric region (Fig. 4). Frequency distributions of body temperatures were negatively skewed, as shown by the fact

that the median temperatures were always higher than the means, indicating that occasionally exceptionally cold snakes were encountered.

Multiple regression showed oral temperatures of *T. radix* to depend most strongly upon light intensity, air temperature and substrate temperature (Table 3). Cloacal temperatures of *T. radix* depended most strongly upon the same three environmental factors. Of these three factors air temperature was most important. Oral temperatures of *T. sirtalis* also depended most strongly upon light intensity, air temperature and substrate temperature. Habitat exerted an additional effect upon oral temperatures of *T. sirtalis*, over· and above that produced by the other environmental factors, oral temperatures being lower in the closed marsh. Cloacal temperatures of *T. sirtalis* depended most strongly upon air temperature and substrate temperature and were independent of light intensity. Cloacal temperatures, like oral temperatures, were lower in the closed marsh, other environmental factors being equal. An additional effect seemed to be exerted upon the cloacal temperatures of *T. sirtalis* by substrate moisture and time of capture, cloacal temperatures being higher at moist capture sites and lower near mid-day, other factors being equal. The relationships of oral and cloacal temperature to the habitat factor differed significantly (P < .01) between *T. radix* and *T. sirtalis*, being negative for *T. sirtalis* only. The relationships of cloacal temperature to substrate moisture, substrate temperature and time of capture differed significantly (P < .01) between *T. radix* and *T. sirtalis*, being more positive for *T. sirtalis*.

Activity. – A bimodal pattern of daily activity was suggested by daily profiles of catch per search hour in the field for both *T. radix* and *T. sirtalis* in the allopatric region (Fig. 5). Effort in this region ranged from 3 to 22 search hours per hourly time interval. In the sympatric region the morning and evening peaks of activity for *T. sirtalis* were farther apart than in the allopatric region, while *T. radix* eliminated its morning peak and became more active towards mid-day. Effort in this region ranged from 4 to 41 search hours per hourly interval and catches were generally lower for both species than in the allopatric region.

DISCUSSION

Feeding Habits. – Both *T. radix* and *T. sirtalis* appeared to feed opportunistically, taking a wide variety of food items in rough proportion to their apparent abundance. This may be considered an adapta-

TABLE 1. Number of *T. radix* and *T. sirtalis* stomachs containing various food items in allopatric and sympatric regions.

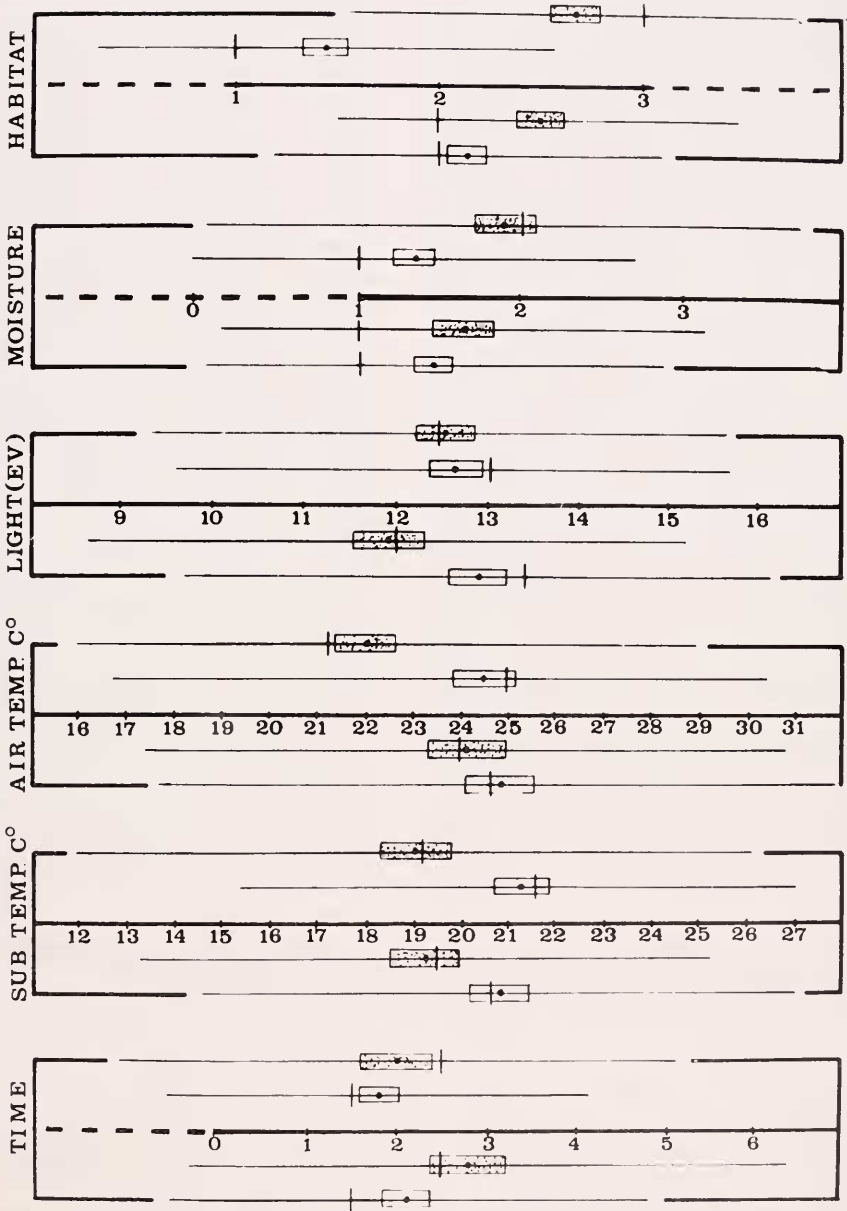| FOOD CLASS	Allopatric Region		Sympatric Region	
	T. radix	*T. sirtalis*	*T. radix*	*T. sirtalis*
Rana sylvatica	24	15	36	24
Rana pipiens	4	0	3	0
Pseudacris triseriata	8	11	7	4
Hyla versicolor	2	2	1	3
Bufo	3	3	4	2
Tadpoles	5	0	1	0
Rodentia	1	0	1	0
Oligochaeta	5	2	0	0
Hirudinea	6	6	6	0
Gastropoda	0	0	2	0

Fig. 2. Location of *T. radix* (open rectangles) and *T. sirtalis* (stippled rectangles) on gradients of the six environmental factors measured at capture sites. Rectangles indicate 95% confidence intervals on the means (solid circles). Medians (vertical lines) and 95% confidence intervals on the observations (horizontal lines) are also shown. The axis of an environmental factor is broken beyond the measured range of that factor. Statistics above the axis pertain to the allopatric region. Statistics below the axis pertain to the sympatric region.

    Time is measured in units of hours ± 2 P.M. Habitat code 1 = pond; 2 = open marsh; 3 = closed marsh. Moisture code 1 = dry; 2 = damp; 3 = waterlogged; 4 = standing water; 5 = open water.

tion to the short growing season encountered in the temperate zone. In contrast to the studies of Carpenter (1952), Fouquette (1954) and Fleharty (1967), who worked with different species combinations, no differences were found between the feeding habits of *T. radix* and *T. sirtalis* in sympatry. Gregory's (1977a) limited observations on the feeding habits of *T. radix* captured largely in sympatry with *T. sirtalis* invited similar conclusions. Although *T. sirtalis* altered its feeding habits in the sympatric region, it did not do so in such a way as to displace its niche from that of *T. radix*. The major changes involved an increased utilization of wood frogs and a decreased utilization of chorus frogs. These changes may have been the result of variations in the relative availability of wood frogs and chorus frogs. Since there was no niche displacement in sympatry with respect to feeding habits, the changes cannot be attributed to species interaction. White and Kolb (1974), in their study of two garter snakes species in California, similarly rejected the hypothesis of competitive displacement since changes in the feeding habits of *T. sirtalis fitchi*, when in sympatry with *T. elegans*, were not in the direction of niche displacement. They felt that feeding habits were determined largely by availability, which interpretation is also suggested in the present study.

Enviornmental Factors. – In the allopatric region, habitat, air temperature and substrate temperature contributed most strongly to niche discrimination (Table 2). *Thamnophis radix* occurred near ponds at high air but low substrate temperatures while *T. sirtalis* occurred near marshes at lower air but higher substrate temperatures. Although univariate comparisons between *T. radix* and *T. sirtalis* also attributed importance to substrate moisture, multivariate results indicated that this factor was superfluous due to its strong correlation with other environmental factors of greater value in discriminating between species. Substrate temperature was a particularly strong negative correlate of substrate moisture.

The ecological importance of habitat can be related to the thermal responses of the snakes. Habitat exerted an independent effect upon both oral and cloacal temperatures of *T. sirtalis*; this was probably due to the shade provided by the sedge mat in the closed marsh. Large expanses of sedge mat with associated stands of aspen forest provide a readily accessible thermal refuge. This type of cover may have been particularly important to *T. sirtalis*, which is more darkly colored than *T.*

TABLE 2. Discriminant function coefficients (unstandardized) and indices of discriminating value derived from them in allopatric and sympatric regions.

ALLOPATRIC	Habitat	Moisture	Light	Air Temp.	Sub. Temp.	Time	R_c^{2*}
Coefficient	-30.729	-2.922	2.021	1.110	-1.227	-1.703	.54
Index**	- .502	- .066	.085	.117	- .103	- .069	
SYMPATRIC	Habitat	Moisture	Light	Air Temp.	Sub. Temp.	Time	R_c^{2*}
Coefficient	-6.117	-0.243	1.660	-0.105	0.577	-0.661	.25
Index**	- .163	- .010	.142	- .022	.104	- .055	

[*] R_c^2 = Squared cannonical correlation coefficient (fraction of variation in species membership accounted for by the discriminant function)

[**] Standardized discriminant function coefficients multiplied by R_c^2.

radix in the Interlake district and perhaps subject to overheating in the summer (Hart, 1975). Such cover was conspicuously absent from the pond habitat utilized extensively by *T. radix*. Cover was similarly important to niche discrimination in the studies of Carpenter (1952) and Fleharty (1967).

The importance of air and substrate temperature to niche discrimination in the allopatric region also reflects the thermal relations of the snakes. Both factors exerted a strong effect upon oral and cloacal temperatures of *T. radix* and *T. sirtalis*. Since *T. radix* is lighter in color than *T. sirtalis* in the Interlake district, it may have been better adapted to the higher air temperatures that characterized its range and able to tolerate them by seeking out low substrate temperatures. *Thamnophis sirtalis* was apparently unable to tolerate high air temperatures without a thermal refuge in the form of closed marsh or aspen forest and, probably for this reason, it did not occur much beyond the range of these habitat types. Fleharty (1967) similarly found air and substrate temperatures to be useful in defining the niches of garter snake species.

In the restricted sympatric region, the available range of environmental factors was probably reduced. As a result, the importance of habitat and air temperature to niche discrimination was also reduced, the latter becoming insignificant. However, the importance of substrate temperature and light intensity at capture sites was increased (Table 2). This can only be interpreted as a behavioral reaction of the snakes, but need not be explained as a reaction to the presence of another species. It may represent compensation for changes in the available niche, *T. radix* seeking out higher light intensities and substrate temperatures to compensate for lower available air temperatures in the sympatric region; *T. sirtalis* seeking out lower light intensities and substrate temperatures to compensate for higher available air temperatures in the sympatric region and for the scarcity of shade normally afforded by the closed marsh and forest of its allopatric habitat.

One of the ways in which this selection could have been accomplished is suggested by the daily profiles of catch per search hour. In the allopatric region, both species showed a roughly bimodal activity pattern with morning and evening peaks. In the sympatric region, however, *T. radix* was most active during mid-afternoon close to the hottest part of the day, and *T. sirtalis* was active earlier in the morning and later in the evening, apparently avoiding the heat of mid-afternoon. This increased difference between the activity patterns of *T. radix* and *T. sirtalis* in the sympatric region was illustrated by univariate comparisons of time to capture, coded to reflect midday activity. The difference in time of capture between *T. radix* and *T. sirtalis* was increased in the sympatric region, but was not great ($.05 > P > .01$). Multivariate results virtually eliminated the increased importance of this factor in the sympatric region indicating that the activity shift was entirely due to the selection of higher light intensities and substrate temperatures by *T. radix* and lower ones by *T. sirtalis*.
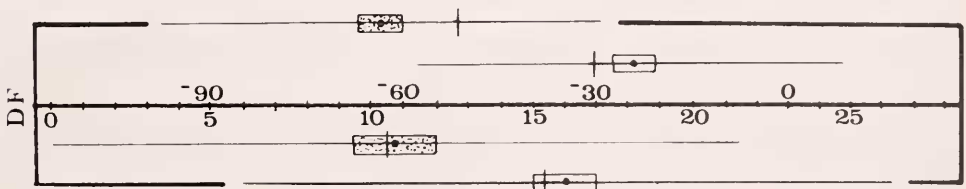

Fig. 3. Location of *T. radix* and *T. sirtalis* on the axes of the discriminant functions (DF) derived from seasonally adjusted data in allopatric and sympatric regions. Symbols and format as in *Fig. 2*.

These changes in selection of light intensity and substrate temperature must represent behavioral adjustments other than those reflected in the daily activity pattern.

MacArthur and Levins (1967) showed that when ecological similarity surpasses a minimal limit, interspecific selective forces act to produce competitive niche displacement. While the relative niche positions of *T. radix* and *T. sirtalis* changed in the sympatric region, there was no net displacement of the niches occupied (Fig. 3). This does not preclude a competitive interaction since there was probably an increased similarity of the available niches. It does, however, suggest that competitive interaction was of minor significance if it occurred at all. The relationship between limiting similarity and resource availability in competitive interactions has been discussed by May (1974), Riebesell (1974) and Pianka. 1974). Schoener (1974) has pointed out that resource availability is an unmeasured variable in most studies of resource partitioning. Measurement of niche separation relative to the available niche breadth was not attempted in the present study due to the difficulty of quantifying an available as opposed to occupied niche with respect to the environmental factors considered.

Thermal Relations. – The higher body temperatures of *T. radix* in the allopatric region (Fig. 4) suggest that this species has a slightly higher preferred temperature than *T. sirtalis*. Such a difference would correlate well with differences in thermal tolerance. *Thamnophis sirtalis* is reported to have a slightly lower minimum critical temperature than *T. radix* (Fitch, 1965). Vincent (1971) found *T. Sirtalis* hibernating at body temperatures as low as $-3°C$ while Bailey (1949) did not find *T. radix* to survive hibernation at temperatures lower than $-2°C$. While cloacal body temperatures of *T. sirtalis* upon capture were slightly lower than those reported by Fitch (1965) as "preferred", body temperatures of reptiles captured in the field are often found to be lower than preferred temperatures (Licht et al., 1966) due, perhaps, to greater catchability at sub-optimal temperatures.

In spite of the ecological adjustments made by both species in the sympatric region, in apparent compensation for marginal air temperatures, body temperatures became more similar there. This was primarily due to an increase in the body temperature of *T. sirtalis*, which probably indicates that *T. sirtalis* had passed its limit of behavioral thermal adjustment and may explain why it was unable to pene-
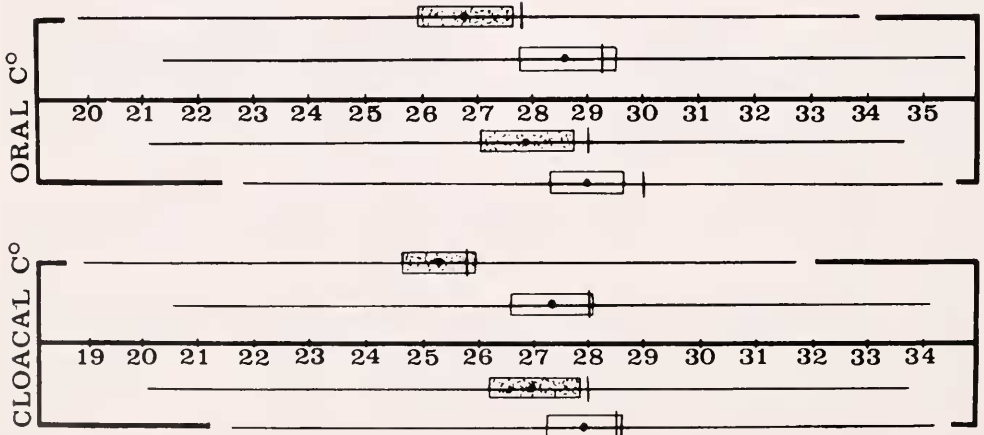

Fig. 4. Oral and cloacal temperatures of *T. radix* and *T. sirtalis* in allopatric and sympatric regions. Symbols and format as in *Fig. 2*.

trate further into the range of *T. radix*. Body temperatures of *T. radix* were not altered appreciably in the sympatric region, and in fact showed a very slight increase in spite of the fact that *T. radix* there was at the northern periphery of its range. *Thamnophis radix*, therefore, had not passed its limit of behavioral thermal adjustment, but was probably at or very close to this limit in the sympatric region. Neither *T. radix* nor *T. sirtalis* would have been able to alter their activity patterns much further since *T. radix* was already concentrating its activity in the hottest part of the day and *T. sirtalis* had virtually eliminated its mid-day activity.

Negative skewness in the frequency distributions of reptilian body temperatures is often reported (Cowles and Bogert, 1944; Brattstrom, 1965). As Heath (1964) points out, although this pattern is often interpreted as indirect evidence for a photophobic reaction at body temperatures higher than the modal one, similar patterns are produced by inanimate objects incapable of movement, and need not be attributed to behavioral thermoregulation. The significance of the pattern in the body temperature distributions of *T. radix* and *T. sirtalis* is, therefore, uncertain.

The oral and cloacal body temperatures of *T. radix* and *T. sirtalis* depended most strongly upon air temperature (Table 3) and next most strongly upon substrate temperature. Fleharty (1967) related cloacal temperatures of *T. elegans*, *T. cyrtopsis* and *T. rufipunctatus* primarily to substrate temperature and found little effect due to air temperature. However, Fleharty measured air temperature 24 cm above ground level rather than immediately above ground level as in the present study. He measured substrate temperature right at ground level so that it represented the combined effects of air and substrate temperature as measured in the present study. Gregory (pers. comm.) found cloacal temperatures of *T. ordinoides*, *T. elegans* and *T. sirtalis pickeringi* to depend strongly upon both air and substrate temperatures; the latter, measured immediately below ground level, exerted the greatest effect.

Oral temperatures of both *T. radix* and *T. sirtalis* depended strongly upon light intensity. While the cloacal temperatures of *T. radix* also depended upon this factor, those of *T. sirtalis* did not. This may be explained by the fact that *T. sirtalis* was often captured on the sedge mat of a closed marsh, with its head above the mat

TABLE 3. Regression equations for dependence of oral and cloacal temperatures on environmental factors [$Y = I + (H \times \text{Habitat}) + (M \times \text{Moisture}) + (L \times \text{Light}) + (A \times \text{Air Temp.}) + (S \times \text{Sub. Temp.}) + (T \times \text{Time})$]

	T. radix		*T. sirtalis*	
Y:	Oral	Cloacal	Oral	Cloacal
I	6.941	-1.620	4.420	-0.113
H	0.259	0.222	-1.081**	-1.090**
M	-0.485	-0.525	1.460	3.048**
L	0.626*	0.358*	0.448*	0.073
A	0.448*	0.513*	0.536*	0.635*
S	0.165*	0.164**	0.273*	0.382**
T	-0.239	-0.210	0.029	0.333**

*Partial regression coefficient non-zero (P <.01)
**Partial regression coefficient non-zero and different from that of the other species (P <.01)

and its tail below, shaded from the sun. Light intensity was not measured under the sedge mat.

Oral and cloacal temperatures of *T. sirtalis* were influenced by habitat. The protection from the sun offered the snake by the sedge mat and forest of the closed marsh habitat probably explains this effect.

The direct effect of substrate moisture upon the cloacal temperatures of *T. sirtalis*, other factors being equal, may have been due to relative humidity near the substrate, which was not measured. a direct effect of relative humidity upon body temperatures of reptiles, due to inhibition of evaporative cooling, was suggested by Cowles and Bogert (1944). Relative humidity was probably high under the sedge mat of a closed marsh. Such an effect probably is not completely explained by the habitat factor since there was considerable variability in the moisture of a closed marsh between the edges and the center.
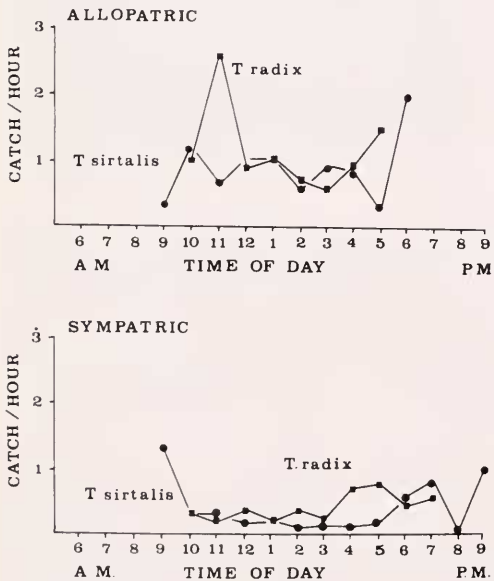

Fig. 5. Profiles of catch per search-hour calculated for hourly intervals throughout the course of the day. Profiles are shown for *T. radix* (solid squares) and *T. sirtalis* (solid circles) in allopatric and sympatric regions.

The direct effect of time of capture, coded as a deviation from mid-day, upon the cloacal temperatures of *T. sirtalis* is difficult to interpret. Diel variations in other measured environmental factors such as light intensity, air temperature and substrate temperature cannot, in a multiple regression, explain an independent effect due to time of capture. Such variations would, in a simple regression, be expected to result in an inverse rather than direct relationship between body temperature and time of capture, with higher body temperatures closer to mid-day. The observed effect of time of capture upon the cloacal temperatures of *T. sirtalis* over and above those produced by variation in other measured factors suggests either the influence of unmeasured environmental factors exhibiting a diel cycle or an intrinsic diel cycle in cloacal temperature.

Activity. – The degree of bimodality in the daily activity pattern of *T. radix* was found by Heckrotte (1962) to be temperature dependent. A similar temperature dependence appears in the daily activity patterns of both *T. radix haydeni* and *T. sirtalis parietalis* (Hart, 1975) and explains the opposite adjustments in activity pattern made by *T. radix* and *T. sirtalis* in the sympatric environment (Fig. 5) and the increased importance of time of capture in discriminating between the niches of *T. radix* and *T. sirtalis* in this region. By becoming most active near mid-day, *T. radix* was able to select higher light intensities and substrate temperatures. By avoiding the heat of mid-day, *T. sirtalis* was able to select lower light intensities and substrate temperatures. Jordan (1967), on the basis of a small sample of snakes from roads within a region of sympatry in Minnesota, similarly found *T. sirtalis* to be active earlier in the morning and later in the evening than *T. radix*.

Competitive Interaction and Density-Dependence. – The primary importance of physical as opposed to biotic factors in the ecology and evolution of temperate zone animals and plants has been stressed by Dobzhansky (1950) and Fischer (1961). Bogert (1949) suggested that this was especially true of northern poikilotherms

and noted that stringent thermal requirements might prevent specialization with respect to density-dependent ecological factors. The importance of thermal factors to northern reptiles has been illustrated by Gregory (1977b) who attributed the disappearance of the youngest year class at a communal den of *T. sirtalis* to reproductive failure brought on by a cool, cloudy summer. It is illustrated in the present study by the fact that ecological adjustments made by both *T. radix* and *T. sirtalis* at their range peripheries involved those niche parameters most strongly related to body temperatures. Marked reduction in the relative frequency of *T. sirtalis* captures following spring flooding of many of its dens during the present study further emphasizes the significance of climatic factors in regulating populations of northern reptiles. These factors act independently of density and often catastrophically. The similar feeding habits of *T. radix* and *T. sirtalis* in Manitoba and the lack of evidence for niche displacement between them suggest that density-dependent factors such as competitive interaction are probably not important to northern poikilotherms enduring a harsh continental climate. However, the food partitioning among three *Thamnophis* species on Vancouver Island (Carr and Gregory, 1976; Gregory, 1978) is suggestive of competitive interaction. Such density-dependent factors may be important to northern poikilotherms in maritime regions where the climate is more moderate.

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